

Effect of relative humidity on foliar absorption of P and Rb by *Chrysanthemum* and *Pilea* *

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Abstract

Air humidity differentially affected the foliar absorption of ³³P and ⁸⁶Rb by *Chrysanthemum morifolium* 'Giant # 4 Indianapolis White' and *Pilea cardierei*. As the relative humidity increased from 47 to 80% in most cases, there was an increase in uptake. Further raising of humidity to 92% increased uptake of Rb and P by *Chrysanthemum* leaves only when guttation did not occur. Air humidity influenced most strongly the uptake of calcium phosphate probably due to its low solubility.

INTRODUCTION

Foliar absorption of substances is dependent upon environmental factors such as relative humidity. Generally there is an increase in uptake with an increase in relative humidity (Babiker and Duncan, 1975; Marczyński and Jankiewicz, 1978a; b; Prasad et al., 1967; Sachs et al., 1967) but exceptions have been found (Morton, 1966; Teubner et al., 1957; Westwood and Batjer, 1960). Therefore this research was done to clarify the relationship between relative humidity and foliar uptake of P and Rb.

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MATERIALS AND METHODS

Methods were similar to those described earlier (Marczyński and Tukey, 1986). Rooted cuttings of *Chrysanthemum morifolium* 'Giant # 4 Indianapolis White' and *Pilea cardierei* were grown in a greenhouse in a Hoagland's nutrient solution containing half-strength P and K until 2-3 new leaves had developed. One day before treatment the plants were placed in growth chambers with a day-night temperature of $22^{\circ}\text{C} \pm 1^{\circ}\text{C}$, light intensity of $2 \times 10^4 \text{ lx} \pm 1 \times 10^3 \text{ lx}$, and 16-hour day length, conditions which were maintained throughout the experiments. In experiments requiring relative humidities above 80%, plants were placed in transparent plastic tents built within the growth chamber. A humidifier and two fans were placed in the tent to increase humidity and to maintain air circulation; the floor was also kept constantly wet.

The upper or the lower surface of the third leaf from the apex was treated in the middle of the day with 20 μl of 10 mM rubidium phosphate, pH 7.5, which was double labelled with ^{33}P and ^{86}Rb . In one experiment, rubidium phosphate, pH 5.0 was also applied and in another calcium (pH 5.0) and ammonium phosphate (pH 8.0) were used. At the end of the treatment period, usually 48 h, a 1.35 cm diameter disk encompassing the treated area of the leaf was removed with a cork borer. The remainder of the plant was ashed and assayed for radioactivity as described previously (Marczyński and Tukey, 1986). In some of the experiments, the disks punched from *Pilea* leaves were washed, and radioactivity in the disks after washing was determined. Total uptake was the radioactivity remaining in the disks after washing plus radioactivity translocated from the treated spot to other plant parts.

Each treatment had 5-10 replications. After angular transformation, data were subjected to analysis of variance; Tukey's W-procedure was used for comparing treatment means (Steel and Torrie, 1960). Plant water potential was measured with a Plant Water Status Console Model 3005, Soilmoisture Equipment Company.

RESULTS

Greater amounts of both ^{33}P and ^{86}Rb were absorbed through the abaxial leaf surfaces of *Pilea* than the adaxial surfaces. For example, 80-90% of the ^{33}P and 60-70% of the ^{86}Rb applied to the abaxial leaf surface were absorbed as compared with 3-5% of the ^{33}P and 20-25% of the ^{86}Rb through the adaxial surfaces (Table 1). Less than 1% of the ^{33}P and 20% of the ^{86}Rb applied to the adaxial surface of *Pilea* leaves was translocated from the treated area to other plant parts within 48 h

Table 1

Effect of relative humidity on absorption of ^{33}P and ^{86}Rb with 10 mM rubidium phosphate by *Pilea* leaves for 48 h

Air humidity	^{33}P				^{86}Rb			
	absorbed total in %		absorbed and translocated in %		absorbed total in %		absorbed and translocated in %	
	adaxial surface	abaxial surface	adaxial surface	abaxial surface	adaxial surface	abaxial surface	adaxial surface	abaxial surface
78% RH growth chamber	4.85	83.79	0.77	12.24	25.25	58.14	21.50	42.32
80% RH plastic tent	4.31	86.00	0.57	14.97	20.57	65.20	16.50	47.05
91% RH plastic tent	3.25	90.03	1.00	14.71	19.56	69.85	11.33	51.48

No significant differences were found between means within the same column at $P = 0.01$.

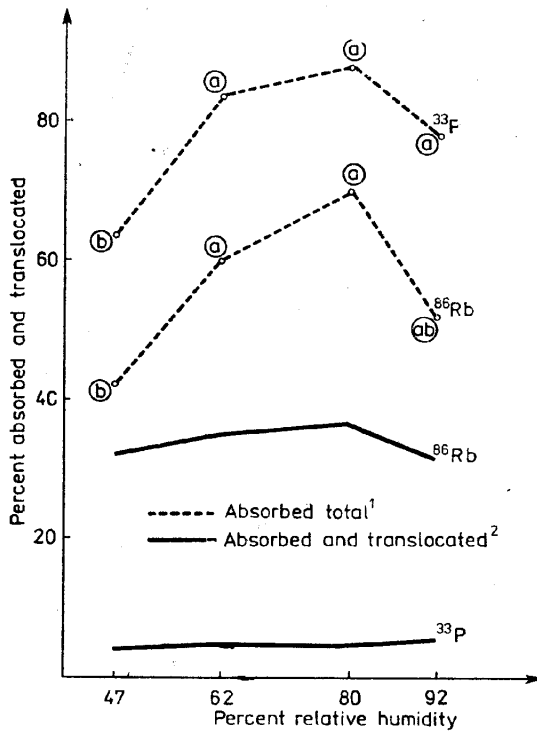


Fig. 1. Effect of relative humidity on absorption and translocation of ^{33}P and ^{86}Rb with 10 mM rubidium phosphate by abaxial surface of *Pilea* leaves. ¹Means on each curve designated by the same letters do not differ significantly at $P = 0.01$.

² There were no significant differences between means at $P = 0.01$

as compared with 14% of the ^{33}P and 51% of the ^{86}Rb applied to the abaxial surfaces. These results are similar to those of previous experiments (Marczyński and Tukey, 1986).

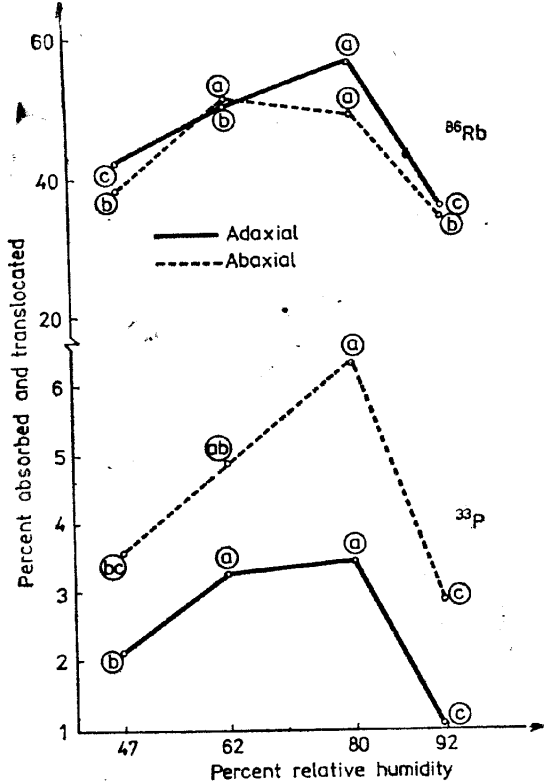


Fig. 2. Effect of relative humidity on absorption and translocation of ^{33}P and ^{86}Rb with 10 mM rubidium phosphate by *Chrysanthemum* leaves. Means on each curve designated by the same letters do not differ significantly at $P = 0.01$

As the relative humidity increased from 47 to 62%, there was an increase in total uptake (radioactivity in treated areas after washing, plus radioactivity translocated to other plant parts) of ^{86}Rb and ^{33}P (Fig. 1). The total amount absorbed for both ^{86}Rb and ^{33}P was higher with the 62% condition but there were no significant differences in contents of ^{86}Rb and ^{33}P outside the treated spots (Fig. 1). When the relative humidity was raised from 62 to 80%, in most cases the increase in uptake was nonsignificant (Figs. 1, 2). Further raising of humidity to 92% decreased uptake and translocation of ^{86}Rb and ^{33}P by *Chrysanthemum* leaves (Fig. 2). A similar trend was found with the lower surface of *Pilea* leaves, but differences were not statistically significant (Fig. 1).

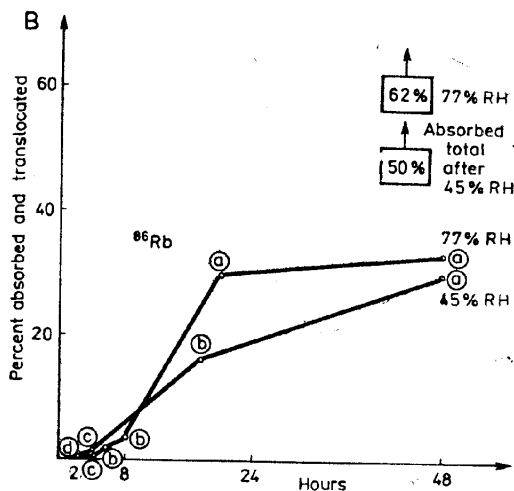
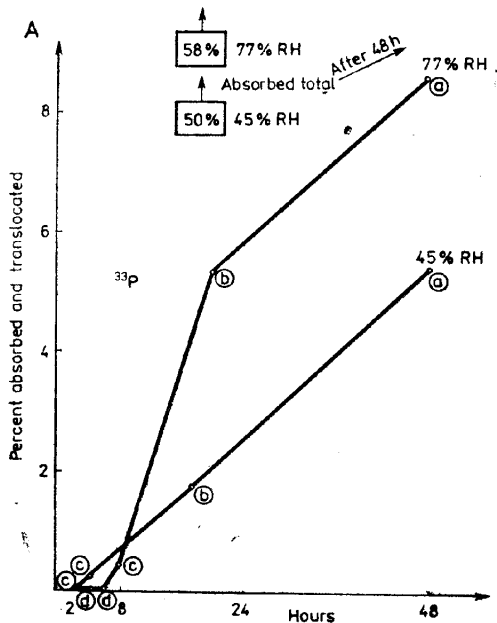


Fig. 3. Effect of relative humidity on absorption and translocation of ^{33}P and ^{86}Rb with 10 mM rubidium phosphate by abaxial surface of *Pilea* leaves. A — absorption and translocation of ^{33}P , B — absorption and translocation of ^{86}Rb . Means on each curve designated by the same letters do not differ significantly at $P = 0.05$. There was a significant difference between humidities at $P = 0.01$. Drying time at 45% RH — 80 min and at 77% RH — 170 min

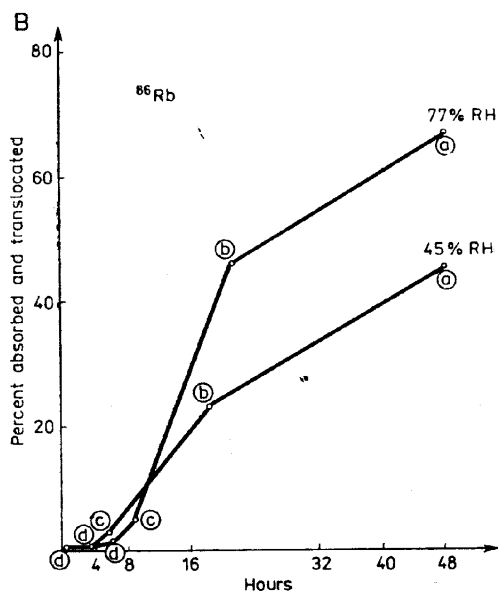
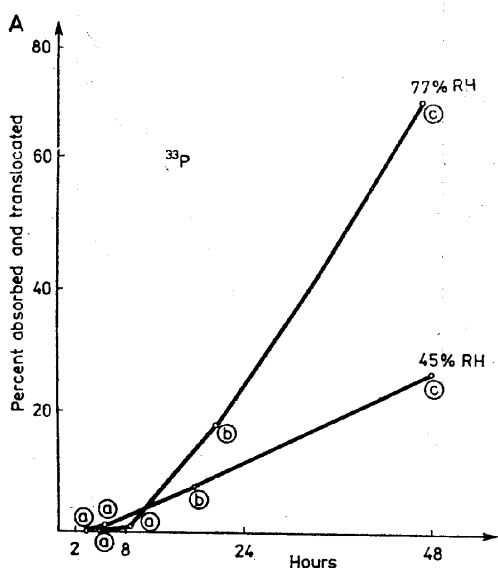


Fig. 4. Effect of relative humidity on absorption and translocation of ^{33}P and ^{86}Rb with 10 mM rubidium phosphate by adaxial surface of *Chrysanthemum* leaves. A — absorption and translocation of ^{33}P , B — absorption and translocation of ^{86}Rb . Means on each curve designated by the same letter do not differ significantly at $P = 0.05$. There was a significant difference between humidities at $P = 0.01$. Drying time at 45% RH — 140 min and at 77% RH — 290 min

The decrease in uptake and translocation at RH of 92% was surprising. Perhaps the treating droplet dried more slowly which resulted in slower increase of radioisotope solution concentration and slower absorption from the droplet. Another possibility could be the change of the CO₂ level in the plastic tent used to attain 92% RH. Some other factors are also not excluded. To check this, two experiments were done with or without plastic tents. In the first one, absorption was compared at the highest (77%) and lowest (45%) relative humidities which could be maintained in the growth chambers without use of a plastic tent. Two to 10 h after application, relative humidity had no significant effect on uptake and translocation of ³³P and ⁸⁶Rb by either *Pilea* or *Chrysanthemum* leaves, although a constant trend to greater absorption and translocation at lower air humidity was observed (Figs. 3, 4). After this initial period, there was an increase in absorption and translocation by both plants at 77% RH, as compared with 45% RH, up to 48 h after treatment (Figs. 3, 4).

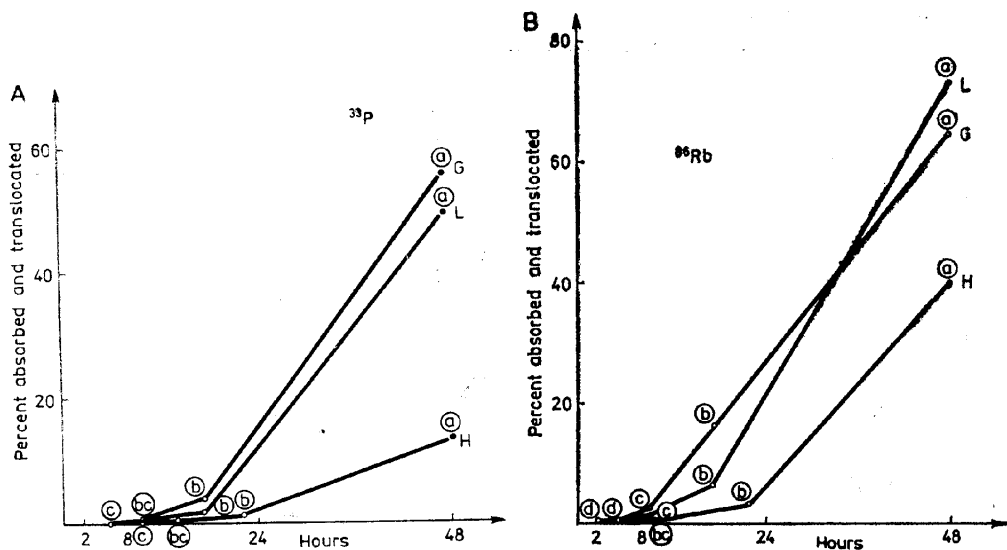


Fig. 5. Effect of relative humidity on absorption and translocation of ³³P and ⁸⁶Rb with 10 mM rubidium phosphate by adaxial surface of *Chrysanthemum* leaves. A — absorption and translocation of ³³P, B — absorption and translocation of ⁸⁶Rb. Means on each curve designated by the same letter do not differ significantly at P = 0.05. There was a significant difference between L and H at P = 0.01 and no significant difference between L and G at P = 0.05. G — growth chamber with 78% RH, L — plastic tent with 80% RH and H — plastic tent with 91% RH. Drying time at G — 5 h, at L — 6 h and at H — 13 h

In the second trial, absorption was compared at the highest (91%) and lowest (80%) relative humidities which could be maintained in two plastic tents built within one growth chamber. To check whether the plastic tent itself had an influence on uptake, plants were also treated in a second growth chamber without a plastic tent, but with temperature, light intensity and relative humidity (78%) very close to that within one of the plastic tents. There was no effect of humidity on uptake by the lower and upper surfaces of *Pilea* leaves, during the 48-h absorption period (Table 1). But in *Chrysanthemum*, less ^{86}Rb and ^{32}P was absorbed and translocated from the treated spot in the higher humidity (91%) than in lower humidity (80%) (Fig. 5), similarly as was noted before (Fig. 2). Further, there were no differences in CO_2 levels in the growth chambers and in the plastic tent placed within the growth chamber. Similarly, there was no difference in uptake and translocation of ^{32}P and ^{86}Rb by both *Pilea* and *Chrysanthemum* leaves in the growth chamber and in the plastic tent within the second growth chamber, both of which were at approx. the same relative humidity (78-89%).

At night in the 91% relative humidity, droplets of guttation fluid were seen on the whole surface of *Pilea* leaves and on the leaf edges of *Chrysanthemum*. During guttation at night the water potential of *Chrysanthemum* was -1.3 bars and in the same humidity during the day was -2.0 bars. For *Pilea* plants it was respectively -1.1 and -2.6 bars. Because the plastic tent did not have an influence on uptake (Fig. 5), and because drying of the droplet could have an influence on uptake only during the first 10 to 20 h (Figs. 3, 4), it was supposed that perhaps the decreases in uptake and translocation at high humidities were in some way related to guttation. To check this, plants were treated within plastic tents with relative humidities of 79% and 92% as before, but with constant light which eliminated guttation. Further, the plants were treated with phosphates with different solubilities.

When guttation did not occur (under constant light) absorption and translocation of both ^{32}P and ^{86}Rb were the same or greater at 92% than at 79% RH (Table 2) independent of the phosphate used. Phosphorus absorption and translocation were particularly increased with increased humidity when *Pilea* and *Chrysanthemum* were treated with calcium phosphate (Table 2), the solubility of which is only 0.5 g/100 g H_2O at 25°C (Linke, 1965). Absorption of ammonium phosphate (solubility 41 g/100 g H_2O at 25°C) by *Pilea* leaves was not affected by humidity. Absorption and translocation by *Chrysanthemum* leaves were higher at 92% than at 79% RH but differences were much less than with calcium phosphate (Table 2).

Table 2

Effect of relative humidity and pH on absorption and translocation of ^{33}P and ^{86}Rb with 10 mM phosphates by *Chrysanthemum* adaxial and *Pilea* abaxial leaf surface for 48 h. Plants were kept under constant light

Phosphate	Air humidity	<i>Chrysanthemum</i>				<i>Pilea</i>	
		^{33}P	^{86}Rb	^{33}P	^{86}Rb		
		absorbed and translocated %	absorbed and translocated %	absorbed and translocated %	absorbed %	translocated %	
Rb-phosphate	79% RH	5.2 c	23.4 b	66.5 bc	6.5 b	42.3 a	31.6 a
pH-5.0	92% RH	13.3 a	53.1 a	82.0 a	13.3 a	42.2 a	37.2 a
Rb-phosphate	79% RH	2.5 a	46.3 a	55.8 a	3.1 c	39.1 a	30.1 a
pH-7.5	92% RH	2.0 d	46.1 a	78.0 ab	4.1 c	45.2 a	32.0 a
Ca-phosphate	79% RH	1.3 d	—	6.7 d	0.9 d	—	—
pH-5.0	92% RH	7.6 bc	—	54.1 c	11.6 a	—	—
NH ₄ -phosphate	79% RH	8.4 b	—	77.3 ab	12.1 a	—	—
	92% RH	12.4 a	—	80.1 a	12.2 a	—	—

Means within the same column followed by a different letter are significantly different at $P = 0.01$.

DISCUSSION

The influence of air humidity on leaf functions including absorption is complex depends on several factors.

In our experiments, rubidium phosphate at pH 7.5 showed a trend to lower absorption in the higher humidity during the first 6-10 h, probably due to slow drying of the droplet. It was reported that prolonged drying of the droplet in higher air humidity increases absorption by extending the time of hydration (Bukovac, 1974; Pallas and Williams, 1962). With compounds with high water retention, such as rubidium phosphate at pH 7.5 (Reed and Tukey, 1978) it is probable that some water can be retained by deposit on the leaf surface during a few hours after visible drying even in low air humidity (i.e. 45%). Acceleration of drying increases the concentration of the treated compound and increases absorption which agrees with work of others (Greene and Bukovac, 1971; Middleton and Sanderson, 1965). In line with this are reports that rewetting a deposit of magnesium (Oland and Opland, 1956), phosphorus (Thorne, 1958), strontium and cesium (Morton, 1966) decreased or did not change leaf absorption, probably due to an effect of concentration. But in some experiments, rewetting increased leaf absorption of strontium (Ambler, 1964), 3-CP (Bukovac, 1965), and Dalapon (Prasad et al., 1962), possibly because these compounds have a lower resistance to complete

drying. In our experiments, rubidium phosphate at pH 7.5 in 77% RH, within 10-20 h after application, exceed absorption occurred in 45% RH (Figs. 3, 4), probably due to complete drying of the droplet in the lower humidity. In 77% RH the compound did not dry completely at least during 20 h and its absorption increased greatly in time.

Some workers reported that solutions containing surfactants were absorbed independently of air humidity (Thompson et al., 1958; Westwood and Batjer, 1960). It is also possible that adding compounds with high solubility may increase absorption. Few workers have reported on the relation between air humidity, solubility, and hygroscopicity of different compounds which Reed and Tukey (1978) have shown to be most important and is demonstrated in this work. Rubidium phosphate at pH 7.5 and ammonium phosphate, which are both soluble in water, were absorbed and translocated in similar quantities as both 79% and 92% RH. Calcium phosphate with its low water retention, was absorbed 6-10 times more at higher humidity than at lower.

It is widely thought that air humidity influences leaf absorption mainly by its effect on cuticle hydration (Ambler, 1964; Babiker and Duncan, 1975; Schönherr, 1976) or by increasing cell water content (Thorne, 1958). But as shown here, the relationship between solubility and air humidity is even more important. Absorption of certain compounds is strongly dependent on air humidity and the ability to form a concentrated film of solution on the leaf surface.

Leaf morphology, including trichomes and cuticle types can influence the air humidity at the surface (Reed and Tukey, 1978) and in this way could modify the influence of the surrounding air humidity on leaf absorption.

It is hard to explain the lower absorption and translocation by *Chrysanthemum* leaves in relative humidity above 90% as compared with 80% (Figs. 2, 5). This difference was noticed only when guttation appeared. Perhaps high root pressure during guttation, which has been demonstrated by high water potential, inhibited absorption. This is supported by the work of Pallas and Williams (1962) who noticed decreased absorption of ^{32}P by bean leaves with an increase in soil moisture tension and root pressure. In addition, it is postulated that guttation is an active process (Häusermann and Wyssling, 1973; Schrept, 1965) which can decrease reserves of ATP and possibly inhibit absorption of ions. In our experiments, the guttation solution did not contain any radioactivity, as was reported by others (Ziegler and Lüttge, 1968), so decreases in absorption were not caused by loss of activity in the guttation fluid.

The *Pilea* plants did not show any influence of guttation or water

potential on P and Rb absorption (Table 1). This could be related to plant specificity as it was reported that *Prosopis juliflora* (Middleton and Sanderson, 1965), a xerophyte, absorbed the same amount of 2, 4, 5-T between 35% and 100% RH.

Humidity can have a very diverse influence on the absorption by leaves. It influences the physico-chemical state of the compound adsorbed on the leaf surface, the physico-chemical state of the leaf surface itself and leaf functions like stomata opening as well as the physiological conditions of the whole plant — its transpiration, gas exchange, root pressure, water conditions of the cells etc. Therefore the effect of increased humidity on absorption differs markedly with different compounds, different external conditions other than humidity and with plant species. This paper shows examples of that diversity.

The very intriguing phenomenon found in this paper — the lowering of absorption in higher humidity seems to have a connection with guttation, but further research is required to explain it.

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Wpływ względnej wilgotności powietrza na wnikanie P i Rb do liści *Chrysanthemum* i *Pilea*

Streszczenie

Wilgotność powietrza w różnym stopniu wpływała na wnikanie ^{32}P i ^{86}Rb do liści *Chrysanthemum* i *Pilea cadierei*. Najczęściej wnikanie zwiększało się, gdy względna wilgotność powietrza wzrastała z 47 do 80%. Jeśli nie wystąpiła gutacja dalsze podnoszenie względnej wilgotności powietrza, do 92%, powodowało zwiększenie pobierania Rb i P. Wilgotność powietrza wpływała najsilniej na pobieranie fosforanu wapnia, przypuszczalnie w związku z jego małą rozpuszczalnością.